

LIMULUS *an* ARACHNID. By E. RAY LANKESTER, M.A.,
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College, London. (With Plates XXVIII and XXIX).

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A. INTRODUCTION AND BIBLIOGRAPHY.

THE prevailing opinion among zoologists at the present day, with regard to the affinities of the King Crab, is that it must be regarded as one of the Crustacea. Even when this view is not fully accepted the King Crab is placed in a special position of isolation and its relationship with Crustacea strongly insisted upon, whilst more remote affinity with the Arachnida is grudgingly admitted.

My friend Edouard Van Beneden, of Liège, is the only zoologist who has definitely taken a divergent line, and has frankly endorsed the instinctive perception of Straus Durkheim in declaring that *Limulus* is no Crustacean, but simply and unreservedly an Arachnid. Ed. Van Beneden bases his opinion upon embryological data. I have elsewhere expressed my full concurrence in that opinion, but the grounds upon which my conclusion rests are not solely embryological—they have reference to the structure of the adult *Limulus* and Scorpion. In the following pages I hope to show that *Limulus* is best understood as an aquatic scorpion, and the Scorpion and its allies as terrestrial modifications of the King Crab.

My views on this subject were formed some eight years ago, and I have to acknowledge the kindness of Mr. Carington, F.L.S., of the Royal Westminster Aquarium, by which I have been enabled to dissect and make histological study of perfectly fresh specimens of *Limulus* sent to me in the living state.

It is not desirable at the outset to follow the history of the discussion relative to the zoological position of *Limulus*. Those who desire to become acquainted with the most important contributions to the subject should consult the memoirs of Anton Dohrn and A. S. Packard, who have given very ample references to the literature of the subject.

I shall here give in alphabetical order a list of the chief works referred to in the following pages, the number attached to an author's name when cited, having reference to the number in the present list. After I have put forward the facts and inferences with reference to the structure and affinities of *Limulus* which appear to me to be well-established, I shall briefly review the various opinions which have been advanced by recent writers of authority.

Special Memoirs.

1. DOHRN, Anton. "Bau und Entwicklung der Arthropoden," 'Jenaische Zeitschrift,' Bd. vi, 1871.
2. GEGENBAUR, Carl. "Anatomische Untersuchung eines *Limulus*," 'Abhandlungen der naturforschenden Gesellschaft in Halle,' 1858.
3. GRÉNACHER. "Unters. über das Sehorgan der Arthropoden," 1879.
4. LANKESTER, E. Ray. "Mobility of the Spermatozoa of *Limulus*," 'Quart. Journ. of Micr. Science,' 1878.
5. MILNE-EDWARDS, Alphonse. "Recherches sur l'Anatomie des *Limules*," 'Annales des Sciences Naturelles,' 5th series, Zoologie, vol. xvii, 1873.
6. NEWPORT, George. "Nervous and Circulatory Systems in Myriapoda and Macrourous Arachnida," 'Philos. Transactions of the Royal Society,' part ii, 1843.
7. OWEN, Richard. "Anatomy of the King Crab," 'Transactions of the Linnæan Society of London,' 1873.
8. PACKARD, A. S., Junr. "The Development of *Limulus polyphemus*," 'Memoirs of the Boston Society of Natural History,' 1872.
9. PACKARD, A. S., Junr. "The Anatomy, Histology, and Embryology of *Limulus polyphemus*," 'Anniversary Memoirs of the Boston Society of Natural History, 1880.
10. VAN BENEDEN, Edouard. "De la place qui les *Limules* doivent occuper dans la classification des Arthropodes," Société Entomologique de Belgique, October, 1871 (translated in the 'Annals and Mag. of Natural History,' 1872).
11. VAN DER HOEVEN. 'Recherches sur l'Histoire Naturelle et l'Anatomie des *Limules*,' Leyden, 1838.
12. WALCOT, C. D. "The Trilobite," 'Bulletin of the Museum of Comparative Zoology at Harvard College,' vol. viii, April, 1881.
13. WOODWARD, Henry. "A Monograph of the British Fossil Merostomata," 'Palæontographical Society of London,' 1866—1878.

Text-books of Zoology.

14. CLAUS, Carl. 'Grundzüge der Zoologie,' fourth edition, first volume, third part, p. 638, 1880.

15. GEGENBAUR, Carl. 'Elements of Comparative Anatomy,' English translation, 1878, p. 230.
16. HUXLEY, Thos. H. 'The Anatomy of Invertebrated Animals,' 1877, p. 260 and p. 374.
17. HAECKEL, Ernst. 'Generelle Morphologie,' vol. ii, p. xc.
18. OWEN, Richard, 'Lectures on Invertebrate Animals,' 1843, p. 181.
19. STRAUS DURKHEIM in Appendix to the sixth volume of the French translation of Meckel's 'Comparative Anatomy,' 1829.

Embryology of Arachnida.

20. BALFOUR, F. M. "Notes on the Development of the Araneina," 'Quart. Journ. of Micr. Science,' vol. xx, 1880.
21. METSCHNIKOFF, Elias. "Embryologie des Scorpions," 'Zeitschrift für Wiss. Zoologie,' Bd. xxi, 1870.

As I am about to endorse the conclusion arrived at by an eminent naturalist of the first half of this century, viz. Straus Durkheim, it will be well to give here at once the grounds upon which he based that conclusion.

Straus Durkheim maintained that *Limulus* should be classified with the Arachnida, but the publication of his views on the subject appears never to have taken a very definite or satisfactory form. In fact the only record of Straus Durkheim's teaching on this subject which I can find is in the French translation of Meckel's 'General Treatise on Comparative Anatomy.' MM. Riester and Alph. Sanson carried out this translation, and added many notes in the form of appendices to each volume. At the end (p. 497) of the sixth volume, which bears the date 1829-1830, there is a note headed, "Sur l'appareil locomoteur passif des Arachnides," which appears to be an abstract of a memoir 'On the Comparative Anatomy of the Arachnida,' read to the Academy of Sciences, June 1st, 1829, but never, I believe, published. M. Straus Durkheim communicated its contents to MM. Riester and Sanson. From this note I submit a few extracts. The authors commence, "La classe des Arachnides, dans laquelle M. Straus comprend le genre *Limule*, formant à lui-seul un ordre designé sous le nom de GNATHOPODES, et dont il isole les PYCNOGONIDES qu'il renvoie aux Crustacés, offre dans la disposition de son squelette et des muscles qui en meuvent les diverses pièces, des particularités tellement tranchées qu'on ne peut y méconnaître un type différent. C'est de ce squelette que sont tirés les traits principaux propres à caractériser la classe des arachnides en general, et qui consiste dans la *disposition des pattes rayonnant sur un sternum commun, dans la présence d'un sternum cartilagineux intérieur, dans l'absence d'antennes.*"

The Arachnida are then divided into three orders, "les pulmonaires, les branchifères, et les trachéens," but it is not explained whether the term "gnathopodes" is to be regarded as simply a synonym of the order "branchifères."

With regard to the internal sternum, the citation of the views of M. Straus runs as follows:—"Dans l'intérieur du thorax de tous les *arachnides*, à l'exception peut-être des *acarides* dont la plupart des espèces sont trop petites pour qu'on puisse les disséquer et connaître leur organisation, on trouve une pièce cartilagineuse diversement configurée suivant les familles, et placée dans le thorax au-dessus du *sternum*. Cette pièce, à laquelle convient le nom de sternum intérieur est maintenue librement par le moyen de plusieurs muscles qui se soudent de différents points de sa surface sur le bouclier, ou sur le sternum extérieur auquel ils se fixent. Elle sert en outre de point d'insertion à un certain nombre de muscles des pattes."

Since the time when Straus Durkheim put forward these views a mass of knowledge has accumulated which has tended to throw light on the affinities of *Limulus*. Of most importance has been the discovery of the complete form of the body of the palæozoic scorpion-like Arthropods known as the Eurypterina, and the quite recent (1873) thorough investigation of the nervous system of *Limulus*, by Alphonse Milne-Edwards, and further, the investigation of the developmental history of *Scorpio*, by Metschnikoff, and of *Limulus*, by Dohrn and by Packard. The gradual growth of the recognition of the Arachnid affinities of *Limulus* during the last twenty-five years is obvious enough, and yet all systematic writers, and all who have especially discussed the question, continue to classify *Limulus* among the Crustacea whilst speculating as to the possible derivation of the Arachnida from that form, or else place *Limulus* in a distinct group, neither Crustacean nor Arachnidan.

I shall endeavour to show in the following pages that there is a much closer agreement of parts between *Limulus* and the Arachnida (especially *Scorpio*) than has been hitherto admitted by any one writer, even by Straus himself. It appears to me that the full extent of the agreement between *Limulus* and the Arachnida has never yet been stated, for whilst this or that observer has recognised *one* set of facts he has overlooked or misinterpreted another, and thus undervalued the indications of affinity between the two forms which he had admitted to exist. That the King Crab is as closely related to the Scorpion as is the Spider

has for years been an open secret, which has escaped notice by something like fatality.

B. COMPARISON OF LIMULUS AND SCORPIO.

The Arachnid which comes nearest in structure to *Limulus* is the Scorpion. In some few points the Spiders and, yet again, the Phrynidæ are more closely similar to *Limulus* than is that animal. I shall proceed, systematically, through a comparison of the skeletal and chief internal organs of *Limulus* with those of *Scorpio*, pointing out where other genera of living Arachnida come into closer agreement with the former than does the Scorpion.

§ *a*. **NERVOUS SYSTEM.**—As the view which may be adopted in regard to the agreement or distinctness of apparently corresponding parts in *Limulus* and *Scorpio* depends, to a considerable extent, on the indications afforded by the nervous system, it will be as well to proceed at once to state what is now known with regard to that system in both *Limulus* and *Scorpio*.

For a long time our knowledge of the nervous system of *Limulus* was very defective, owing to the fact that only badly preserved spirit-specimens had been dissected. Hence it has been held by Van der Hoeven (11) and by Owen (7) that the nerves which supply the first two pairs of appendages take their origin from a nervous mass in front of the œsophagus. Dohrn (1) and Huxley (16), on the other hand, have stated that only the nerves to the first pair of appendages are præ-œsophageal in origin. It was reserved for M. Alphonse Milne-Edwards (5) to demonstrate by the dissection of perfectly fresh specimens of *Limulus* the true arrangement of these parts. I am able, from my own dissection of a fresh specimen of the same animal, to confirm M. Milne-Edward's description, though I must say that such confirmation is a mere formality, since the beautiful memoir in which that author has published his results bears throughout unmistakable evidence of care and accuracy.

With regard to the nervous system of *Scorpio*, we are not in the same favourable position. No zoologist, so far as I am aware, has studied the nervous system, or, indeed, any of the viscera of *Scorpio* by the aid of fresh specimens, and I cannot but expect that some very important modifications, in accepted conclusions, may result from a renewed investigation of the anatomy of that animal carried out upon freshly killed individuals. Nor has the nervous system of the adult Scorpion been studied by the aid of the microscope, in regard to which deficiency we are in the same difficulty so far as

Limulus is concerned in spite of Packard's recent work in that direction (9); in fact, the comparative anatomy of the nervous system of Arthropoda generally has yet to be placed on a firm histological basis, and until this is done we must not attach a very great importance to the results of simple dissection. With regard to the naked-eye appearance of the nervous system of Scorpion, we have, however, the exceedingly careful work of George Newport (6), which is worthy of all confidence, and what is of more importance we have certain embryological data furnished by the investigations of Metschnikoff (21) and of Balfour (20). The observations of the latter zoologist relate to the Araneina, but may fairly be considered as confirmatory of those of Metschnikoff.

The central nervous system of *Limulus* consists, according to M. Alph. Milne-Edwards, (A) of a distinctly emarginated brain or cerebral mass which I have elsewhere proposed to call the ARCHI-CEREBRUM,¹ and of two strands of nervous tissue, which embrace the œsophagus and unite behind it, so as to form (B) an oval œSOPHAGEAL COLLAR, being continued backward from their point of union along the ventral surface of the animal as (C) the ABDOMINAL CORD to a point some distance in front of the anus. The limbs of the collar are united by from three to eight transverse commissures in front of their point of union with one another and behind the œsophagus. From the archi-cerebrum are given off five nerves only, namely, those to the ocelli, to the compound eyes, and to the frontal integument. From the œsophageal collar a great number of nerves radiate, including those to the first as well as to all the other pediform appendages, and also the nerves to the chilaria (or metathoracic sternites) and to the genital operculum. We find a distinct nerve to each appendage, and a number of large tegumentary nerves also given off from the œsophageal collar. It is important to note that the pair of nerves to the genital operculum is derived from this region and not from the cord-like prolongation of the united strands of the collar. It is also important to observe that at present we have no knowledge of the existence of distinct ganglia or enlarged masses of nerve-cells in the œsophageal collar, so that it is not possible to infer from any such fact of structure how many ganglia corresponding to an equal number of segments are represented by the œsophageal collar. M. Alphonse Milne-Edwards, who holds the "chilaria" to be the equivalents of the Scorpion's "pec-

¹ This Journal, April, 1881. 'On the Appendages and on the Nervous System of *Apus cancriformis*.'

tiniform organs," considers that eight pairs of ganglia are thus represented, a pair for each of the walking legs, a pair for the chilaria, and a pair for the genital operculum. The "chilaria" appear to me (as explained below) to be simply "sternites," and not related to the Scorpion's "combs;" and and I should therefore consider only seven pairs of segmental ganglia to be represented in the œsophageal collar. The history of development is not yet quite definitely ascertained, but it should decide this point, and should show, supposing the views which I am about to advocate are correct, that there is no ganglionic enlargement of the cord corresponding to the "chilaria," whilst the ganglionic enlargement from which the genital operculum is innervated should at first be more distinctly abdominal in position, and at a later period become fused with the six ganglion-pairs corresponding to the pediform appendages.

The third portion of the central nervous system of *Limulus* distinguished as the ABDOMINAL CORD, stretches from the œsophageal collar into the abdominal region, and gives off no nerves over a space equalling half its total length; it then enlarges and gives origin to a series of five groups of nerves, of which the first four correspond to and supply the four first pairs of branchial feet, whilst the fifth supplies not only the fifth pair of branchial feet, but also the præanal and perianal regions and the postanal spine. As to the disposition of nerve-cells in this abdominal cord we have no information, that is to say, as to whether it is possible anatomically to define separate ganglia in connection with the five groups of nerves in its hinder part, or in any region in front of them.

A very important relation between the arteries of *Limulus* and the main nerve trunks was first indicated by Owen (18), but more fully elucidated by Alphonse Milne-Edwards. This consists in the *ensheathing* of the œsophageal collar and of the abdominal cord in an actual arterial trunk; not only this but many of the larger nerves (those to the limbs) are ensheathed also by branches of the same arterial trunk. M. Milne-Edwards has pointed out that this arrangement is most nearly approached in *Scorpio*, and has recognised the remarkable agreements between the arterial system of the two animals—to which reference will be made further on—though he nevertheless is led by other considerations which are, I think, erroneous, to refuse to *Limulus* a position among the Arachnida.

When we compare the nervous system of *Scorpio*, as far as it has been made known by Newport and Metschnikoff,

with that of *Limulus* we find portions precisely corresponding to the three main regions above distinguished in the latter animal. Anteriorly we have (A) a cerebral mass supplying the central and marginal eyes with nerves, (B) a large œsophageal collar, from which radiate the nerves to the appendages and some other parts, and (C) an abdominal cord which terminates in the fourth of the narrow præanal segments of the body.

When we look into details a little more closely we find some very obvious differences between these regions as presented in the Scorpion on the one hand and in *Limulus* on the other. But it must be remembered, in regard to these differences, that we have no account of the Scorpion's nerve-centres derived from the dissection of fresh specimens, nor of the actual arrangement of nerve-cells and nerve-fibres as revealed by microscopic examination.

In the first place the brain and the œsophageal collar of *Scorpio* are more intimately fused with one another than are the corresponding parts of *Limulus*. Moreover, the œsophageal collar is relatively more massive, and exhibits but a small perforation for the passage of the very narrow œsophagus. Instead of being bridged over behind the œsophagus by transverse commissures, as in *Limulus*, the two halves of the collar appear to be flattened out here and fused with one another. It is possible that a more accurate knowledge of this region in *Scorpio* might show structure representing the transverse commissures of *Limulus*.

A long tract of the most anterior portion of the abdominal cord in *Scorpio*, as in *Limulus*, gives off no nerves. But in accordance with the elongated form and well-marked segmentation of the hinder region of the body, we find that after this first tract there are, in *Scorpio*, seven well-marked ganglia placed at intervals on the cord, the most anterior of them sending off nerves to the *third* pair of lung-sacs, but to nothing in front of this.

With regard to the actual origin of nerves, it has always been stated that the first pair of appendages of *Scorpio* receive each a nerve from the præ-œsophageal ganglion. If this were absolutely the case it would mark a considerable difference between *Scorpio* and *Limulus*. But as a matter of fact mere inspection of Newport's drawing is sufficient to show that the nerves to the chelicerae of the Scorpion have a lateral position embracing the true "archi-cerebrum," which supplies the lateral and central eyes between them, and whatever may be the result to be obtained in the future by microscopic sections or study of fresh specimens, we have

the important embryological fact due to Metschnikoff (and confirmed for other Arachnida by Balfour) that the nerve-ganglion mass from which the nerve to the chelicera on each side takes its origin is *quite independent of the archi-cerebrum*, and in the embryo is placed behind the latter, and to the side of the œsophagus right and left. This seems to me sufficient to justify a complete assimilation of the two regions in Scorpio and Limulus, the difference being merely that post-embryonic fusion of the archi-cerebrum and lateral ganglia has proceeded a little further in Scorpio than in Limulus.

From the collar, then, in Scorpio, as in Limulus, the nerves to all six of the pediform appendages take their origin. But the agreement extends even further than this, for the nerves to that region of the Scorpion's body which corresponds with the genital operculum of Limulus also proceed from the œsophageal collar. The *attraction* (if I may use the term) of nerve origins to the œsophageal collar appears to have proceeded further in the Scorpion than in Limulus, for, whereas, in Limulus, the first and remaining four pairs of branchial feet are supplied from the abdominal cord, in Scorpio those parts, which for reasons to be given below, I consider to represent the first, second, and third of the branchial feet of Limulus, all appear to receive their nerves from the œsophageal collar, so that it is not until we come to the representatives of the fourth pair of branchial feet of Limulus (*viz.* the third pair of lung-books, see below) that we find in the Scorpion a nerve supply from the abdominal cord. This phenomenon of the travelling forward and concentration of nerve origins and their connected ganglia is one sufficiently familiar in various groups of animals. The fact of the dislocation in this way of the nerve supply of the genital operculum of Limulus above remarked on, receives illustration by the still further carrying out of the same process in Scorpio.

The difference in the disposition of the nerve organs (such as it is) in regard to the *hinder* part of the abdominal cord in the two animals receives its explanation from the difference of general form and segmentation of the hinder region of the body which they respectively exhibit.

It appears, then, that there is when the most recent results of anatomical and of embryological observation are taken into consideration, no important difference between the central nervous system of Limulus and of Scorpio, and more especially it is to be noted for the purpose which we have next in view, *viz.* that of comparing the skeleton and appendages of the two animals, that there is not a difference of

origin in the large nerves supplying the appendages, or the genital or the respiratory region, which can forbid us from unreservedly accepting as exactly representing one another, parts, which on the ground of numerical sequence, appear to reciprocally correspond.

§ 6. SKELETON.—I. Tergites, or Dorsal Sclerites.—It is difficult to separate the description of one part of the skeleton

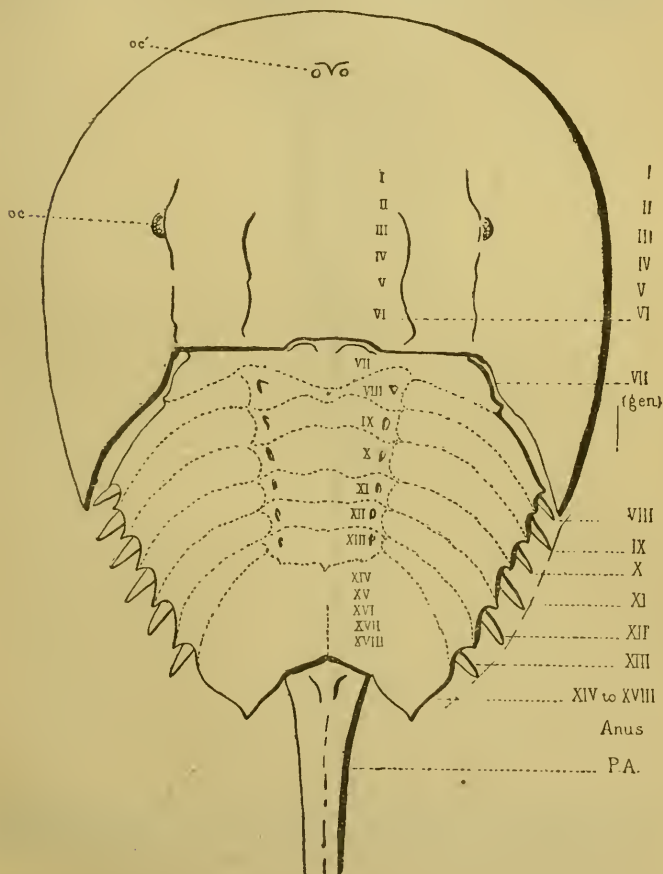


FIG. 1.—Outline of the tergal surface of *Limulus polyphemus* (drawn from the object). The dotted lines correspond to the markings on the abdominal carapace, which in the adult indicate what were separate segments in the embryo. *oc'*. Simple eyes (mesial). *oc*. Compound, or grouped eyes (lateral). *P.A.* Post-anal spine.

of *Limulus* and *Scorpio* from that of another, and in com-

mencing with the tergal elements, we must necessarily refer simultaneously to the general disposition of the appendages.

Cephalothoracic tergites.—In *Limulus* (woodcut, fig. 1),¹ as in *Scorpio* (woodcut, fig. 2), the anterior region of the body is covered in by a large sclerite, which is known as the cephalothoracic plate or carapace.

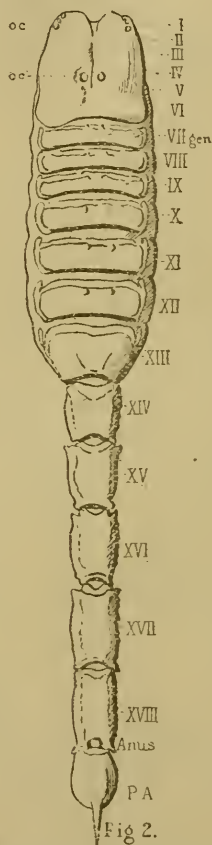


FIG. 2.—Outline of the tergal surface of a scorpion, *Butkus Kochii* (drawn from the object). *oc'*. Simple eyes (mesial). *oc*. Grouped eyes (lateral). *P.A.* Post-anal spine. The anus is on the sternal surface.

In *Limulus* its margins are produced and its posterior angles extended, so as to produce a form which differs from

¹ It is necessary to state once for all that where not otherwise expressed I always allude by the term *Scorpio*, or *Scorpion*, to the species *Butkus Kochii*, of India, which happens to have been that studied by me. Other species differ in trifling details from this.

that seen in the Scorpion, but in essential points there is remarkable agreement. In both the carapace carries two paired groups of eyes. Nearer the middle line is a single pair of simple eyes (*oc'*), which in *Scorpio* have an almost central position; more laterally placed (quite laterally in *Scorpio*) is a group, on either side, of simple eyes (*oc*), which in *Limulus* are so closely aggregated as to form what is often called "a compound eye." The compound eyes of *Limulus* have, however, been shown by Grenacher (3) to differ very much in structure from the compound eyes of either Crustacea or Insects, to which they have usually been assimilated. They are more correctly interpreted—as the comparison with *Scorpio* would suggest—as an aggregation of simple eyes. Such an aggregation (varying, according to the genus, in number from two to five) we find in a less compact form than in *Limulus* on the right and left side of the Scorpion's cephalothoracic tergite.

In both *Limulus* and *Scorpio* the cephalothoracic tergite covers in an area corresponding to the six leg-like appendages which are present in both animals, and may therefore be considered as representing six coalesced tergites (I to VI). In *Limulus* the genital operculum which follows upon the legs, and also the metathoracic sternites or chilaria which lie between it and the bases of the last pair of legs, have been by some morphologists regarded as also indicating segments which should be reckoned to the cephalothorax, and accordingly eight coalesced tergites have been supposed to constitute the carapace of the King Crab, whilst only six can be reckoned for the Scorpion. In reality, however, the chilaria are not appendages at all, as is proved by their late appearance in development (Packard, 8) and their form; they are simply sternites corresponding to the pentagonal sternite placed between the bases of the last pair of legs in *Scorpio* (woodcut, fig. 5). As to the genital operculum of *Limulus*, though in the adult it is in some measure adherent to the region of the cephalothorax, yet it has a tergal area corresponding to it in the *abdominal* carapace, and in the embryonic *Limulus* is clearly seen to belong to that region, and not to the cephalothorax. The innervation of the genital operculum from the œsophageal nerve-collar has, as already pointed out, no weight as an argument in favour of the association of that coalesced pair of appendages with the cephalothorax, for on the very same grounds it would be necessary to associate a large part of the middle region of the Scorpion's body (as far as and inclusive of the second pair of pulmonary sacs) with the cephalothorax.

Abdominal tergites.—Following upon the cephalothoracic plate we have in the Scorpion seven wide band-like sternites, to which succeed five narrow cylinders, the dorsal part of each of which is tergite, and solidly fused with the ventral half or sternite. In the last of these twelve segments is placed the anus (in fig. 2 its position is marked, though it is not seen on account of its ventral position), and beyond the anus is the postanal spine or sting.

In *Limulus* (fig. 1), in place of the seven band-like and five half-cylindrical tergites, we find one large chitinous plate, which is known as the "abdominal carapace." In its posterior region is placed the anus, and to it succeeds a postanal spine, sometimes, but erroneously, compared to the cylindrical segments of the Scorpion's body. Clearly enough the postanal spines in the two cases correspond to one another.

If there is correspondence between *Limulus* and *Scorpio* of segment for segment and piece for piece throughout (as it is the purpose of this essay to demonstrate), then in the abdominal carapace of *Limulus* we must find the representatives of the twelve segments, which in the Scorpion exist between cephalothorax and anus. The embryonic *Limulus*, as has been shown by Dohrn and Packard, exhibits in this region of the body a series of *separated* segments, which fuse together as growth advances, and constitute the one immovable abdominal carapace. In the adult the indications of the former existence of these separate segments is more obvious than has been supposed. In fig. 1 I have indicated by dotted lines the series of ridges, which can be made out in the abdominal carapace of an adult *Limulus polyphemus*, and which clearly mark off a number of the original segments.

With regard to the general form of this region as compared with the body of the Scorpion, it may be pointed out that here, just as in the region of the cephalothorax, there is an excessive development and exaggeration of the margin of the dorsal integument, so that the central area marked out in the figure is the real "body" of the *Limulus*, and the wide spreading lateral areas are only enormous excrescences of a relatively superficial character. It is not difficult to find numerous parallels to these pleural developments in all groups of Arthropoda.

Returning to the examination of the actual number of segments indicated in the abdominal carapace of the adult *Limulus*, we find areas corresponding to the seven wide tergites of the Scorpion marked in the drawing of *Limulus* by the numbers VII to XIII. Corresponding to these areas

are a series of marginal processes, the first corresponding to the first area, is a mere angular process of the integument, but the six which follow are in the form of movable spines.¹

Corresponding also to the six segments which bear the six spines (that is, to the six hinder segments of the seven in question) are a series of pits in the axial region of the tergum, a pair in each segment.

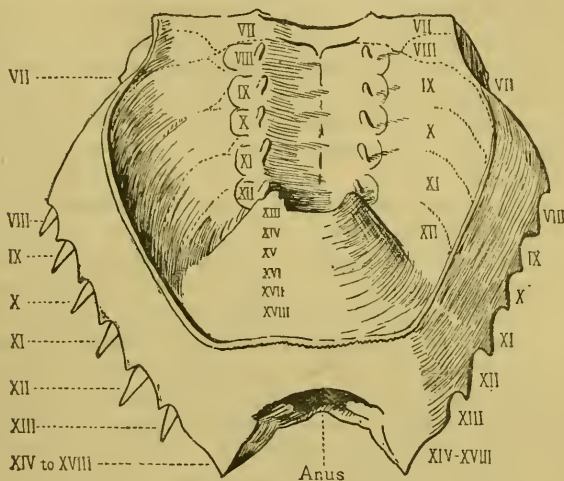


Fig 3.

FIG. 3.—View of the abdominal carapace of *Limulus polyphemus* from below, the soft sternal region and appendages of the anterior six segments and the viscera having been removed.

The figures VII to XII upon the drawing (drawn from the object) are placed by the sides of the tergal entapophyses. The continuation of the same series (XIII to XVIII) is placed upon the chitinated sternal surface of the unsegmented region, which in *Limulus* represents the seventh abdominal and the five cylindrical præanal segments of the Scorpion.

These are deep invaginations of the integument forming hollow processes, pushed as it were into the body cavity and clothed internally with cartilage, the structure of which has been described by Gegenbaur (2); they give attachment to muscles and are well termed "entapophyses" by Owen (7).

When we look in the abdominal carapace of *Limulus* for representatives of the five cylindrical præanal segments of the Scorpion, we find nothing but a broad smooth area extending from the marking which indicates the hind

¹ These spines I have seen slowly moving, independently of one another, in the living King Crab, indicating a separate musculature for each spine.

border of the thirteenth segment (seventh of the abdominal series) to the soft membrane which forms the hinge of the postanal spine.

In the embryo *Limulus*, however, this area is further segmented. We do not find the five segments of the Scorpion, but we find two of which (as segments) no indication is left in the adult, and the foremost of these carries a movable spine on each side like those in front of it.

The anterior margin of the segment or tract of the body which carries the anus appears to be uniformly in Arthropoda, and in some other segmented animals, the part from which new segments grow and become individualised, and it is to this tract of the body including its præ- and postanal regions that the name "telson" is applicable as, for example, in the Lobster. It not unfrequently happens that this segment-producing region does not produce the full number of segments in given examples of an Arthropodous class, which is characteristic of the majority or of the more fully segmented members of the class. Thus, both in Crustacea and Arachnida we find numerous forms with a reduced number of abdominal segments.¹ Usually, however, as in the spiders, the embryo exhibits at some time of its development the full complement of segments, the hindmost of which subsequently become obliterated by fusion or atrophy. *Limulus* so far conforms to this plan as to show the segmental potentiality of its præanal area, but fails to exhibit to the observer the full complement of segments even as a temporary arrangement of its living substance.

Accordingly the whole area posterior to the ridge marking the posterior border of the thirteenth segment may be regarded in *Limulus* as belonging to the "telson," or area of potential segmentation, a certain reservation being observed in respect to the one or two minute segments which appeared and disappeared in this region in the embryo.

We may, when comparing this condition of things with that exhibited by the Scorpion, *either* consider the telsonic area and spine of *Limulus* as representing the five cylindrical segments and the sting of the Scorpion in an unsegmented state, *or* we may insist rather upon the actuality than the protentiality, and identify the telson or fifth of the cylindrical segments of the Scorpion (*viz.* that carrying the anus), and the postanal spine with the telsonic area and spine of *Limulus*, whilst regarding the four anterior cylin-

¹ Note also the evanescent character of the three last segments of *Thelyphonus* (fig. 12).

dric segments of the Scorpion as something over and above and not developed in *Limulus* at all.

It seems, however, probable from the evidence of extinct forms, as well as from the abortive segmentation of the embryo, that *Limulus* is *not* derived from an ancestor in which the telsonic area was as limited in its production of segments as it is in *Limulus* itself, but on the contrary, that the ancestor of *Limulus* had the full complement of segments (and possibly more) which is seen in *Scorpio* and the *Eurypterina*. In that case the præanal area and spine of *Limulus* would not merely be an area representing the five cylindrical segments and sting of *Scorpio* in *potentiality*, but would be the *actual* representative of those segments gradually reduced and fused in the course of an historic process of change.

II. Appendages.—At each stage of the comparison between *Limulus* and *Scorpio*, the proofs of the intimate affinity of the two animals become more convincing, since we find that the view which it is necessary to adopt in order to make one set of structures agree closely in the two animals, is precisely the view which it is necessary to adopt, when a second set are considered, in order to make agreement possible.

We have just dealt with the tergites and have found an exact correspondence of piece for piece, with the exception that four præanal segments are suppressed or five fused in *Limulus* which are discretely present in *Scorpio*. In order to admit such an agreement of piece for piece as to tergites, we have to reject the view that the chilaria and the genital operculum represent segments belonging to the cephalothoracic tergite, for in that case the cephalothorax of *Scorpio* would be a fusion of six, whilst that of *Limulus* would be a fusion of eight pieces.

When we come to examine the sternites, we shall find that the exclusion of the chilaria from the series of appendages is exactly what is required in order to identify the sternites of *Limulus* with those of *Scorpio*, and the removal of the genital operculum of *Limulus* from the cephalothorax makes its identity with the genital operculum of *Scorpio* even more obvious than it would otherwise be.

The six pairs of appendages of the cephalothorax of *Limulus* may be compared one by one with the six pairs of *Scorpio*.

Cephalothoracic appendage, No. I.—We have already disposed of the obstacle which has been always raised hitherto when the chelicerae of the Scorpion have been

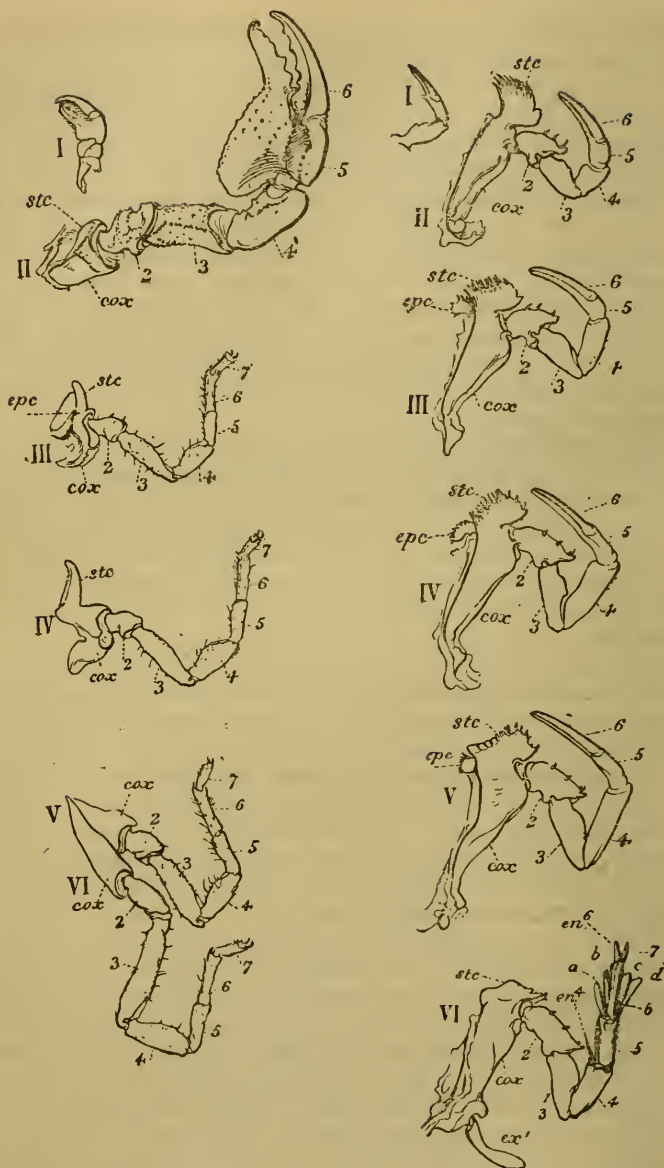


FIG. 4.—Cephalothoracic appendages of *Scorpio* (left), and of *Limulus* (right), drawn from the object. *cox*, coxa. *stc*. Sternocoxal process of the coxa. *epc*. Epicoxite. *ex'*. Exite of the coxa of the sixth appendage of *Limulus*. *en'*. Endite of the fourth segment of the same limb. *a*, *b*, *c*, *d*. Endites and exites of the fifth segment of same. *en⁶*. Endite of the sixth segment of the same.

assimilated to the chelicerae or first pair of limbs of *Limulus*. Instead of there being a difference as to innervation we have seen that there is a real identity.

In *Limulus*, each of the first pair of appendages is a short pair of nippers (woodcut, fig. 4, I, right) composed of three sclerites; at the base of the two appendages and between them and the mouth is placed an ovate sternite, the camerostome or upper lip. (Plate XXVIII, fig. 4).

In *Scorpio* (woodcut, fig. 4, I left) a similarly small pair of appendages is found similarly composed of three sclerites, and similarly overhanging an oval "camerostome."

Ceph. thor. app., No. II.—In this and the following leg-like appendages of *Limulus* six chief sclerites are developed, the basal one or "coxa" being much enlarged, and its interior border produced into a well-marked process provided with tooth-like hairs. The arrangement of the limbs around the mouth and the central sternite which follows it (*pmst* in Pl. XXVIII, fig. 4), is such that the processes of the coxae of all ten limbs act together as manducatory organs. The process of the coxa may be called "the sterno-coxal process" (*stc.* in the woodcut, fig. 4). The second cephalo-thoracic appendage in the female *Limulus polyphemus* is like the third, fourth, and fifth, a chela—that is to say, the penultimate sclerite is produced so as to form with the last sclerite a pair of nippers. In the male this is not the case, the second pair of appendages being thicker and heavier than in the female, and the penultimate joint not prolonged. The form of appendage seen in the male *L. polyphemus* in this position is similar to appendages seen in other Arachnida than *Scorpio*, viz. *Thelyphonus* (woodcut, fig. 12).

The second pair of appendages in the Scorpion is like that of the female *Limulus*, but relatively larger. It consists of six sclerites as in *Limulus*, and has a sterno-coxal process on its coxa, which acts with its fellow of the opposite side as a jaw (woodcut, fig 4, II).

Cephalo-thoracic appendage, No. III.—In *Limulus polyphemus* this has, in both sexes, the same form as has the second appendage in the female. It is similarly composed of six sclerites, but in addition to these we find a distinct movable sclerite developed on the median border of the coxa. This sclerite may be termed the "epicoxite" (woodcut, fig. 4, III, *epc.*, right). The epicoxite is a remarkable feature, and is not easily paralleled among Arthropoda. The basal "endite" of the limbs of the Crustacean *Apus* is similar to it, and perhaps derived from a common ancestral origin.

In *Scorpio* the third cephalothoracic appendage is in the form of a walking leg, and as such has seven sclerites. It is a remarkable fact that in *Limulus* the sixth cephalothoracic appendage, which is non-chelate, also presents seven axial sclerites (woodcut, fig. 4, vi, right), so that the Scorpion's ambulatory limbs do not depart from the possibilities of *Limulus* in developing axial sclerites beyond the number six. It is also important to notice in this connection that the *Arachnida* exhibit a great variability in the number of joints present in their legs. *Thelyphonus* develops a four-jointed "tarsus" at the end of the five proximal segments of its ambulatory limbs (woodcut, fig. 12), whilst *Galeodes* presents a curious increase in the number of segments in the proximal region of its hinder limbs (woodcut, fig. 10).

The most important feature in which the third and subsequent cephalothoracic limbs of *Scorpio* resemble those of *Limulus* is in the great development of the coxæ. The sterno-coxal process is present on the third and fourth cephalothoracic appendages, and is even larger relatively than in *Limulus*. In the third and fourth limbs it is free, overlying a very soft minute sternal region below the mouth, and playing with its fellow of the opposite side the part of an ingestive organ for the mouth. The narrow cleft between the opposed sterno-coxal processes probably acts by capillary attraction in the taking up of such food as the blood of other animals.

The coxæ of the fifth and sixth appendages of *Scorpio* have, on the other hand, no free sterno-coxal process.

The great enlargement of the coxæ of these four pairs of appendages, and their encroachment upon the median area, is accompanied by, and related to, the suppression of any representative of the sternal sclerite (*pmst.*, fig. 4, Pl. XXVIII) which is present in *Limulus*. The coxæ of the third pair and of the fourth pair meet one another in the middle ventral line, but are separated by soft membrane. The coxæ of the fifth and sixth pairs do not meet their fellows in the middle line, but are kept apart by the wedge-shaped extremity of a sternite (*met.* in woodcut, fig. 8). They differ from the coxæ of the third and fourth pairs in that the fifth is adherent to the sixth (woodcut, fig. 4, v, vi, left.)

The base of the third appendage in *Scorpio* exhibits a development internal to the sterno-coxal process, which corresponds to, and probably represents, the "epicoxite" of *Limulus*. This is in the form of a movable plate (woodcut, fig. 4, III, *epc.*, left), which presents parallel ridges on its surface.

Cephalothoracic appendage, No. IV.—Appendage No. iv

in *Limulus* closely resembles No. III. As in No. III, an epicoxite is present.

The corresponding appendage of *Scorpio* has been already mentioned. It has seven joints and a large sterno-coxal process, but no epicoxite, such as occurs in the limb next in front of it.

Cephalothoracic appendage, No. V.—In *Limulus* this resembles Nos. III and IV, like them having an epicoxite.

In *Scorpio*, No. V, is a seven-jointed ambulatory limb, with large coxa fused to the coxa of the next following appendage, but devoid of sterno-coxal process.

Cephalothoracic appendage, No. VI.—In *Limulus* this is the characteristic digging limb, unlike in the special modification of its parts and their remarkable function (for which see the citations of Lockwood and of Lloyd in 'Owen's Memoir,' No. 7) any other arthropod appendage.

In structure it is remarkable for exhibiting the feature of secondary movable arthrites diverging from the axis of the limb, unusual in Arthropoda other than the Crustacea. Seven axial sclerites or segments can be distinguished, the coxa being large, as in the other limbs, but devoid of an epicoxite. On the other hand, whilst the "endite" is thus absent, an "exite" is developed in the form of a flattened elongated piece articulated to the external border of the coxa (woodcut fig. 4, VI *ex'* right).

The second and third segments of the axis are devoid of apophyses, but the fourth bears a large spine-like articulated endite. The fifth joint of the axis carries four flattened apophyses (endites and exites), which are articulated and capable of active movement. The sixth joint bears one articulated endite, and, further, the short terminal seventh or ultimate segment of the axis, which is relatively much longer in newly hatched individuals than in the adult.

The sixth cephalothoracic appendage in *Scorpio* is quite similar to the three preceding walking legs. Its large coxa is fused to that of the fifth appendage of the same side. The spinous outgrowths on the sixth and seventh segments of this and the other legs are in character somewhat similar to the more highly developed apophyses of the digging limb of *Limulus*.

The seventh pair of appendages or genital operculum.—In *Limulus* lying between the bases of the sixth pair of cephalothoracic appendages is a pair of sclerites, the chilaria of Owen, actually the metathoracic division of the sternum (woodcut fig. 5, *st.* right), which belongs to the segment carrying the sixth pair of appendages. Precisely similar in position

in *Scorpio* is a pentagonal¹ sclerite divided into a right and a left half by a median groove (woodcut fig. 5, *st* left upper figure). This is, in like manner, the metathoracic sternite, of which more will be said below.

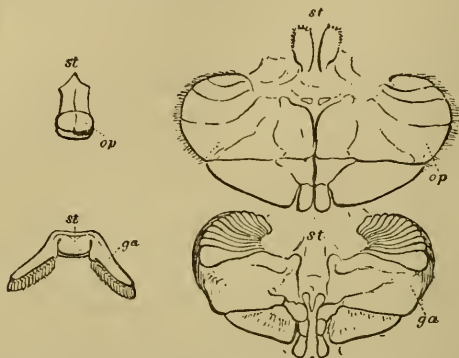


FIG. 5.—The seventh (*op*) and eighth (*ga*) pairs of appendages of *Scorpio* (left) and *Limulus* (right), together with the thoracic metasternites (*st* of the upper figures), and sternites of the eighth segment (*st* of the lower figures). The anterior face of the appendages is shown. Drawn from the object.

Following in *Limulus* as in *Scorpio* upon the metathoracic sternite, is a lid-like plate, the hinge of which is transverse to the long axis of the body, and on the inner face of which are placed, both in *Scorpio* and in *Limulus*, the genital apertures, male or female, as the case may be (woodcut fig. 6, VII, right *Limulus*, left *Scorpio*).

The history of development in *Limulus* shows that this genital operculum starts as two independent processes of the body, which are to be regarded as the appendages of the seventh segment. The operculum retains throughout life evidence of its double origin, and closely resembles in form the five succeeding pairs of appendages which carry the respiratory lamellæ.

In *Scorpio*, on the other hand, the genital operculum is relatively of very small size, as seen in figs. 5 and 8 *go*; in fig. 6, it and the following appendages are drawn on an enlarged scale for the purpose of comparison with the corresponding parts in *Limulus*. Very little trace of having been formed by the union of two lateral appendages is exhibited by the genital operculum of *Scorpio*. At the same time its

¹ Pentagonal in the subgenus *Buthus*, from which my drawings and notes are taken, but more triangular and reduced in size in the subgenus *Androctonus*.

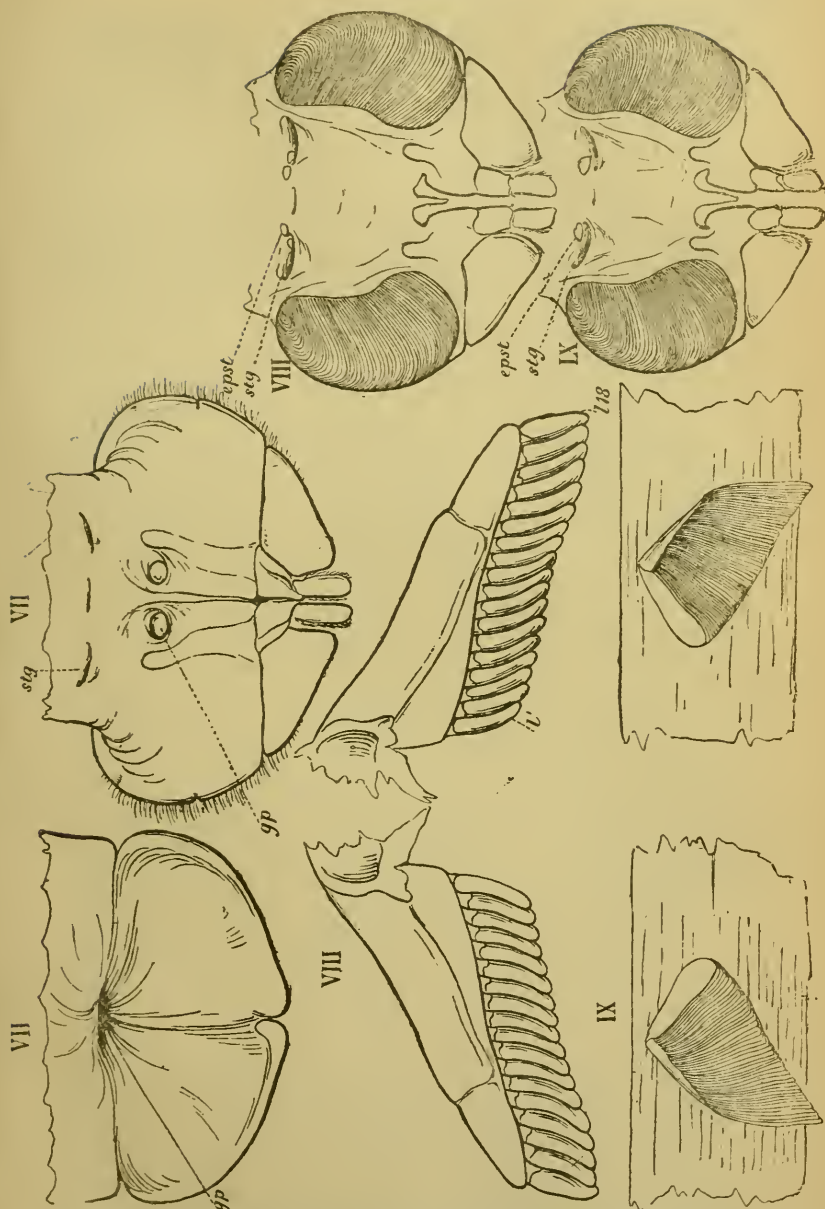


FIG. 6.—The seventh, eighth, and ninth pairs of appendages of *Scorpio* (left) and *Limulus* (right). The posterior face of the appendages is shown. *gp*. Genital pore. *stg*. Parabranchial muscular stigmata (tendons of the thoraco-branchial muscles) of *Limulus*. *epst*. Epistigmatic sclerites of same. Drawn from specimens.

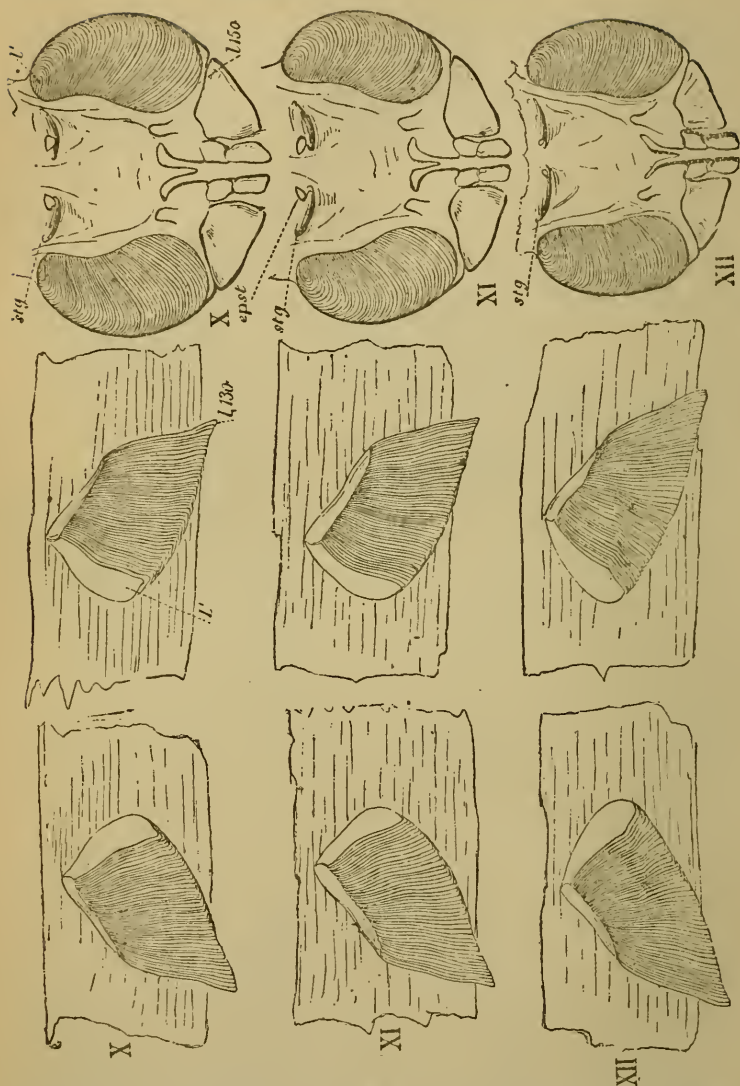


FIG. 7.—The tenth, eleventh, and twelfth pairs of appendages of *Scorpio* (left), and of *Limulus* (right). The posterior face of the appendages is shown. *stg.* Parabranchial stigmata of *Limulus*. *epst.* Epistigmatic sclerites. *l.* Mediad, or first lamella of the lamelligerous appendages. *l130.* External, or one hundred and thirtieth lamella of the same in *Scorpio*. *l150.* External, or one hundred and fiftieth lamella of the same in *Limulus*. Draw from specimens. It is important to note that in these and other figures the lung-books of the Scorpion are represented as entirely freed from the delicate pulmonary sac which invests them.

bifid margin speaks of such an origin, and, as a matter of fact, such appears to be its embryological history.

I shall here quote a passage from 'Balfour's Embryology,' recounting Metschnikoff's observations upon the existence of rudiments of appendages in the segments of the Scorpion's body following upon the cephalothorax with its six pairs of limbs. The observations have great importance, not only in reference to the genital operculum but also in regard to the pulmonary sacs and their "branchial books" which are found in succeeding segments.

Balfour says, "Rudimentary appendages appear on the six segments behind the ambulatory legs. . . . They persist only on the second segment, where they appear to form the comb-like organs or pectines. The last abdominal segment, *i. e.* that next the tail, is without provisional appendages. The embryonic tail is divided into six segments, including the telson. The lungs are formed by paired invaginations, the walls of which subsequently become plicated, on the four last segments, which bear rudimentary limbs, and simultaneously with the disappearance of the rudimentary limbs" ('Comp. Embryology,' vol. i, p. 359).

Hence it appears that, in Scorpio, in front of the comb-like organs, that is to say, in the position subsequently occupied by the genital operculum, there is in the embryo, as in that of Limulus, a pair of rudimentary appendages. We know that in Limulus these grow together to form the genital operculum. It is in the very highest degree probable that the same history obtains for the similarly related genital operculum of Scorpio.

In discussing the tergites, it has already been pointed out that the genital operculum corresponds to a separate band-like tergite in Scorpio (VII, in woodcut, fig. 2), and to an emarginated area on the anterior border of the abdominal carapace of Limulus (VII, in woodcut, fig. 1), which is more distinctly marked in the embryo.

The eighth pair of appendages.—In Scorpio we find, on the ventral surface corresponding with the eighth tergite (six tergites being reckoned to the cephalothorax) a pair of appendages carrying fine lamellæ set like the teeth of a comb along the inferior margin (woodcuts fig. 5 *ga*, left, and fig. 6 VIII, left; see also Plate XXVIII). They are developed from the second pair of rudimentary abdominal appendages of the embryo.

In Limulus, in the corresponding position, we find a pair of appendages, the first of a series of five pairs (woodcuts fig. 5 *ga*, right, and fig. 6 VIII, right). The appendages of the two sides, as in the case of the genital operculum, do not diverge from one another but are directed towards one another and

united across the middle line by a soft plate-like fold of the sternal integument; the result being that a plate-like body is formed from two originally distinct right and left appendages. On the under surface of each of the combined appendages a series of very delicate lamellæ is found *corresponding to the lamelliform teeth of the Scorpion's comb-like organs*.

Ninth, tenth, eleventh, and twelfth appendages.—In *Limulus*, corresponding to the tergal areas marked IX, X, XI, XII, we find a series of pairs of appendages precisely similar to that belonging to the eighth segment.

In *Scorpio* it will be remembered that in the embryo rudimentary appendages appear corresponding to the first six abdominal segments, or the seventh, eighth, ninth, tenth, eleventh, and twelfth of the whole body. Of these the first pair we have seen, become in all probability the genital operculum; the second pair are known to become the "pectines;" the pairs on the ninth, tenth, eleventh, and twelfth segments *disappear*, as the lung sacs on those segments develop by a process of invagination.

They disappear, but only from view. It has not been shown by actual observation, but it cannot well be doubted, that these rudimentary appendages sink within the lung-invaginations, and become the lamelligerous appendages which are found in them in the adult *Scorpio*.

The four pairs of stigmata on the ventral surface of the ninth, tenth, eleventh, and twelfth segments of the *Scorpion's* body (woodcut, fig. 8) lead into sacs, each of which contains, concealed within it, an appendage consisting of an axis bearing a series of delicate lamellæ (woodcuts, figs. 6 and 7, IX, X, XI, XII, left).

Each of these concealed appendages is strictly comparable in structure to one of the comb-like organs of the eighth segment, the axis corresponding to the axis, and the delicate lamellæ to the teeth of the comb.

Thus, then, we find five pairs of lamelligerous appendages on the five segments of the *Scorpion's* body numbered 8, 9, 10, 11, 12, of which the first pair is external, and accordingly modified, whilst the next four are sunk below the surface, and accordingly modified. In *Limulus*, on the exactly corresponding segments, namely, those numbered 8, 9, 10, 11, 12, we find five pairs of lamelligerous appendages, but these are all external, and all alike modified for the purposes of aquatic respiration.¹

¹ Latreille, though holding the *Limuli* to be Crustacea, and not Arachnida, was the first to insist on the branchia-like character of the *Scorpion's* lung-books

Furthermore, it is important to notice that in *Scorpio* neither in the embryo nor at any other time does the seventh abdominal segment (thirteenth of the whole series) carry a pair of appendages, nor do any of the subsequent cylindrical segments. Similarly in *Limulus* no appendages or rudiments of appendages are to be detected after the last pair of lamelligerous organs—the twelfth of the whole series.

The segmented region, devoid of appendages in the *Scorpio*, is represented by an unsegmented region devoid of appendages in the *King Crab*.

Before entering into a more minute comparison of the lamelligerous appendages of the *Scorpio* with those of *Limulus*, with the object of establishing the identity of origin of the two series by the detection of agreement between them in details of structure, it will be most convenient to examine another series of skeletal elements, namely, the sternites.

III. *Sternites*.—In *Limulus*, in the cephalo-thoracic region, we find that the integument of the sternal area, though to a large extent soft and devoid of hard chitinous plates, yet presents here and there well-marked sclerites. On the sub-frontal area, a small discoidal piece, the sub-frontal sclerite is found (Pl. XXVIII, fig. 4, *sf*). Between the mouth and the bases of the first pair of appendages a much more important sclerite occurs, to which the term used by Latreille for the similarly placed sclerite in *Arachnida*, viz. (camerostome), may be used.

In the *Scorpio* (fig. 8, in front of the mouth to which the line *M* points) a similar tubercular sclerite is found. There is advantage in not merely designating this piece “labrum,” since there is but little ground for holding it to be equivalent either to the labrum of *Insecta* or to that of *Crustacea*.

In the *Spider Mygale* (fig. 9) and in *Galeodes* (figs. 10 and 11, *cam*), this same piece is observed, attaining a remarkable development in the latter.

When we come to the region behind the mouth, we find in *Limulus* a large median sclerite extending from the pharynx backward. It lies between the bases of the third, fourth, fifth, and sixth pairs of cephalothoracic appendages. On account of its position, it may be termed the thoracic promeso-sternite (Pl. XXVIII, fig. 4, *pmst*), since it appears to represent elements which, in other *Arachnida*, are marked off as distinct prosternite and mesosternite.

In *Scorpio* we find nothing corresponding to this piece. By the enlargement and mesiad production of the coxæ of the four hinder cephalothoracic appendages it has been as it were

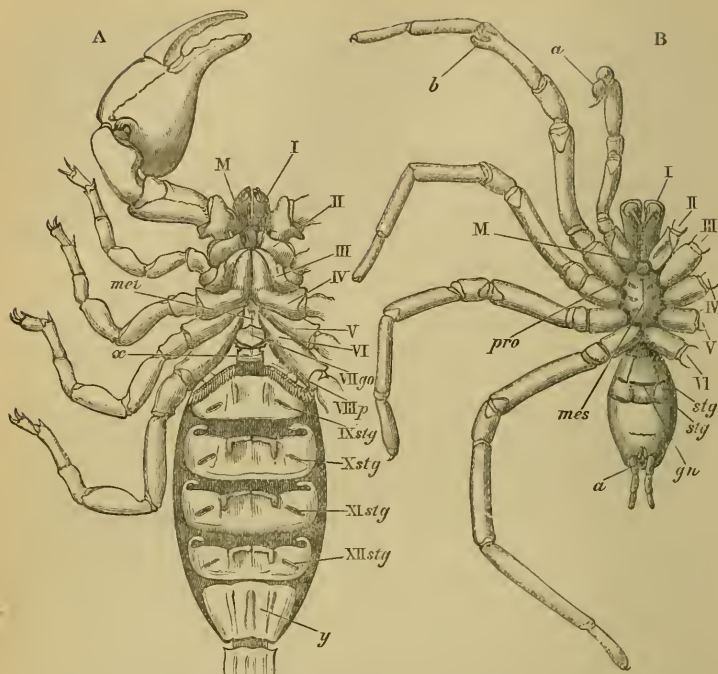


FIG. 8 (A).—Ventral aspect of a scorpion (*Buthus Kochii*), with the terminal segments omitted. Drawn from the object. I to VI. The cephalothoracic appendages. II. Points to the sterno-coxal process of the great chelæ. III. To the sterno-coxal process of the first walking leg. IV. To the sterno-coxal process of the second walking leg. *met*. Thoracic metasternite. VII *go*. The genital operculum. VIII *p*. The pectines, or eighth pair of appendages. *x*. Sternite of the eighth segment. IX *stg*, X *stg*, XI *stg*, XII *stg*. Stigmata leading into the pulmonary sacs, containing the appendages of the ninth, tenth, eleventh, and twelfth segments. *y*. Sternite of the thirteenth segment devoid of appendages. *M*. Mouth, in front of which is seen the camerostome.

FIG. 9 (B).—Ventral aspect of a bird's nest spider (*Mygale* sp), the hairs removed. Drawn from the object. I to VI. Cephalothoracic appendages. *M*. Mouth, in front of which is seen the camerostome. *pro*. Thoracic prosternite. *mes*. Thoracic mesosternite. *stg*. The apertures of the two pulmonary sacs of the left side. *gn*. Genital aperture. *an*. Anus.

obliterated. A similar obliteration has taken place in *Galeodes* (fig. 10), but in *Thelyphonus* (fig. 12), a triangular sternite (*st'*) is found (though erroneously omitted in the figure given in the last edition of Cuvier's 'Regne Animal') in front of the coxæ of the fourth pair of cephalothoracic appendages.

The Arachnids, which come nearest to *Limulus* in the

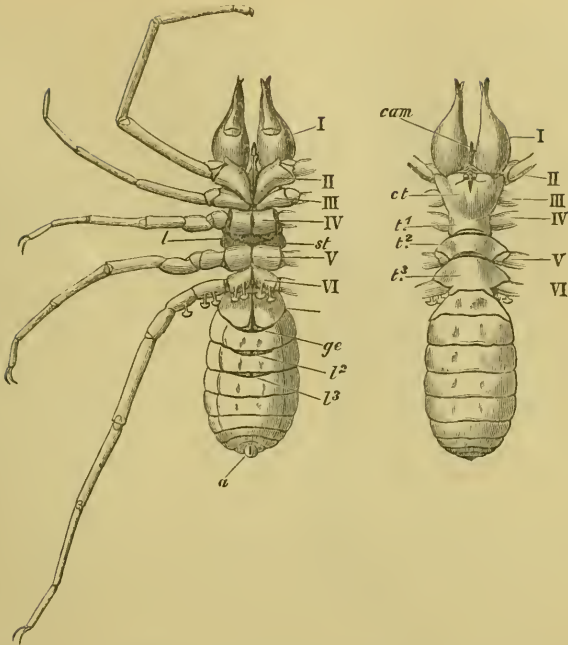


FIG. 10 and 11.—Ventral and dorsal aspect of *Galeodes* sp. (from the object). I to VI. The cephalothoracic appendages. *l*. Thoracic right tracheal aperture. *l*², *l*³. Abdominal tracheal apertures. *ge*. Genital aperture. *st*. Sternal surface. *a*. Anus. *cam*. Camerostome. *ct*. Cephalothoracic tergite. *t*¹. Prothoracic portion of the cephalothoracic tergite. *t*². Separate mesothoracic tergite. *t*³. Separate metathoracic tergite.

character of this portion of the sternal area, are the Spiders. In *Mygale* (*M. avicularia*) the coxæ of the five hinder cephalothoracic pairs of appendages are arranged around a large oval sternite (fig. 9), which is divided into two portions, an anterior small prosternite (*pro*) and a larger mesosternite (*mes*). This double piece appears to correspond to the sternite of *Limulus*, marked *pmst* in fig. 4, Pl. XXVIII.

It is not a little remarkable that, in a structural feature observed in *Limulus* and *not* repeated in *Scorpio* nor in any Crustacean or Insect, the closest parallel should be found in another Arachnid; it is remarkable because it tends still further to determine the association of *Limulus* with the Arachnida in classification rather than with any other group.

Behind the thoracic promesosternite of *Limulus*, separated from it by soft integument and posterior to the coxæ of the

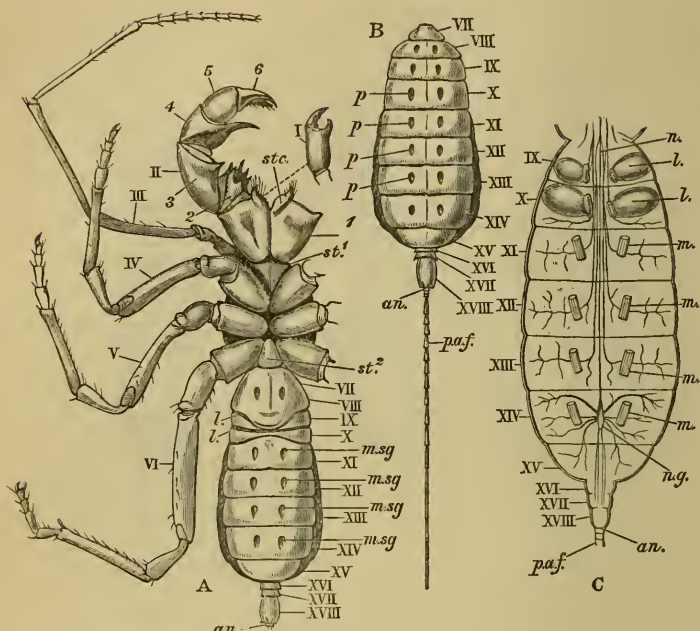


FIG. 12 (A).—Ventral aspect of *Thelyphonus* (from the object). I to VI. Cephalothoracic appendages; the first, which is concealed by the coxa of the second, is represented as removed from its attachment. *stc.* Sterno-coxal process of the coxa of the left second appendage. *st*¹. Thoracic prosternite. *st*². Thoracic metasternite. VII to XVIII. Segments of the abdomen. *l, l.* Apertures of the right lung sacs in the ninth and tenth segments. *msg.* Muscular stigmata on the sternites of the tenth, eleventh, twelfth, thirteenth, and fourteenth segments. *an.* Anus.

FIG. 13 (B).—Dorsal aspect of the abdominal segments of the same. *p.* Muscular pits corresponding to the entapophyses of *Limulus*. *paf.* The jointed postanal filament.

FIG. 14 (C).—Abdominal segments of the same, with the terga and viscera dissected away (after Blanchard). *n.* Nerve cord. *ng.* Abdominal nerve ganglion. *l, l.* Pulmonary sacs in the ninth and tenth segments. *m, m, m, m.* Muscles attached to muscular stigmata of the four following segments. *an.* Anus. *paf.* Postanal filament.

sixth pair of cephalothoracic limbs, we find a pair of closely opposed upstanding sclerites, the chilaria of Owen (*metst* Pl. XXVIII, fig. 4, and woodcut, fig. 4). The late development of these pieces, as determined by Packard, as well as their position, leaves no doubt that they are not to be regarded, as is supposed by some, as rudimentary appendages. They are a paired development of the metathoracic sternal area and may be designated metasternites.

They have no representative in *Mygale* (fig. 9), but here *Scorpio* returns to its allegiance and exhibits a well-developed sclerite exactly corresponding to them. The pentagonal sclerite wedged between the coxæ of the last pair of cephalothoracic limbs in *Scorpio* (woodcut, fig. 8, *met*) clearly enough agrees in position precisely with the chilaria of *Limulus* (see also woodcut, fig. 5). It is true that the form of the pentagonal metasternite of *Scorpio* differs from that of the two little tubercles of *Limulus*, but the exclusion from the functions of the mouth of the former sufficiently accounts for the difference.

In *Thelyphonus* (woodcut, fig. 12, *st.*²) a triangular metasternite corresponding in position to that of *Scorpio* is found.

It is exceedingly astonishing that so careful an observer as M. Alphonse Milne-Edwards should have suggested, as he has done, that the "chilaria" of *Limulus* correspond to the "pectines" of the *Scorpio*, since the former are in front of and the latter are behind the genital operculum. When the possibility of such homologies is entertained, it is but a natural consequence that the complete series of agreements of segment for segment and appendage for appendage which obtains between *Limulus* and *Scorpio*, should be entirely overlooked.

When we pass to the abdominal segments we find a very considerable difference between *Limulus* and *Scorpio* in the development of sternites.

The sternal integument of the region at the base of the genital operculum and the gill-bearing appendages, is almost entirely soft and free from sclerites in *Limulus*. In *Scorpio*, on the other hand, whilst the sternal region around the genital operculum is soft, a well-developed sternite (woodcut, fig. 8 *x*) is found supporting the pectiniform appendages; and for each of the five following segments a broad band-like sternal sclerite is developed. The four anterior of these are perforated, each by a pair of slit-like apertures leading into four pairs of recesses, in each of which a lamelligerous appendage is sunk. The fifth is imperforate, and bears no appendage. The segments of the so-called "tail" which follow present a complete chitinisation of the integument, so that the sternites of each segment is confluent with the tergite.

When we examine the sternal area of the segments of *Limulus* which carry lamelligerous appendages, we find that although the integument is mostly soft and flexible, yet there are small sclerites present, *and, in fact, stigmata or apertures leading into pits corresponding to the stigmata of the pulmonary sacs of Scorpio.*

These parabranchial stigmata of *Limulus* have hitherto

escaped observation.¹ They are found on the posterior face of the median sternal elevation or lobe which unites the two lateral elements or appendages which go to form one of the double lamelligerous organs of that animal (Plate XXVIII, fig. 10 *stg*, and woodcuts, figs. 6 and 7 *stg*). The lips of the stigma are chitinised, and the opening leads into a funnel-like cavity with chitinised walls. The sternal integument further shows one or two small sclerites, the "epistigmatic sclerites" (*epst*), by the side of the stigma. These stigmata occur in the position mentioned, not only at the bases of the appendages of the four segments corresponding to those which carry the pulmonary stigmata in the Scorpion, namely, the ninth, tenth, eleventh, and twelfth, but also at the base of the appendages of the eighth segment, which represent the pectines of the Scorpion, and at the base of the genital operculum. They are connected with the attachment of a series of powerful muscles, the thoraco-branchials, which, taking their origin in the thorax, are inserted into the integument right and left at the base of each of the six pairs of abdominal appendages. The function of these muscles is clearly enough to agitate this series of plate-like organs, either for the purpose of respiration or for that of locomotion, probably for both simultaneously.

The fact that the insertion of a muscle into the integument of *Limulus* is connected with a "cupping" of the area of attachment is remarkable but not without parallel. The series of dorsal entapophyses have a precisely similar significance, and in other Arachnida, *e.g.* *Thelyphonus* (fig. 12 *msg* fig. 13 *p*, and fig. 14 *m*), we find an identical arrangement on both ventral and dorsal surface, the stigmata being, however, much shallower than in *Limulus*.

I am not aware of the occurrence of such "muscular stigmata" in any other Arthropoda than the Arachnida, at any rate, of stigmata comparable to those of *Limulus*. Usually the tendons of muscles are in Arthropoda formed by solid fibrous extensions of the subepidermic layers of the integument.

The tendons or processes connected with the parabranchial stigmata, and with the dorsal entapophyses of *Limulus*, are by no means entirely formed by the invaginated epidermis and its chitinous product. The tissue below the epidermis is developed in a very special manner, and forms part of an endoskeleton which in the thoracic region gives rise to a very remarkable internal sternum or entosternite. The struc-

¹ I communicated an account of their occurrence and probable significance to the Royal Society on May 26th, 1881.

ture of this deep skeletal tissue has been investigated by Gegenbaur, who has shown that it may have the form either of a fibrous or of a more distinctly cartilaginous modification of the connective tissue into which it gradually passes, and from which, on the other hand, is developed in other regions a series of vascular channels constituting the capillaries, veins, and arteries. On the present occasion I do not propose to enter into histological details with regard to *Limulus*, but I may just mention that whilst the hollow entapophyses are invested on their visceral surface by a richly developed cartilaginous modification of the connective substance, with a well developed capsular arrangement of the intercellular substance, the funnel-like invaginations connected with the parabranchial stigmata are clothed and continued by a fibrous tissue not unlike the tendon of Vertebrata. The same tendon-like tissue also forms the entosternite.

In Plate XXVIII, fig. 11, the internal connection of the pair of parabranchial stigmata of a lamelligerous appendage-pair of *Limulus* is drawn. The integument has been dissected away from the whole of the anterior face of the appendages and their uniting sternal bridge, so as to show the inner aspect of the integument of the posterior face. The pouch-like character of the invaginations into which the stigmata lead and the attachment of the thoraco-branchial muscle is thus exhibited. In fig. 13, Pl. XXVIII, one of the funnel-like tendons, consisting internally of chitin borne on epidermis, and externally of fibrous tissue, is shown in an isolated condition. It is possible to introduce a probe into the funnel to the depth of an inch, the axial cavity of invagination extending to that distance. The funnel-like pouch of *Limulus* thus constituted, I consider to be the homologue (that is, the genetic representative or homogen) of the pulmonary sac of Scorpion.

It will now be convenient to give, in a tabular form, a summary of the view which has been set forth in the preceding pages. Having thus exposed what I conceive to be the legitimate conception of the morphological relations of *Limulus* and Scorio, I shall endeavour to justify, by a closer examination, the identification (which forms an essential part of it) of the pectines of the Scorpion and its four pairs of book-like organs sunk in recesses of the integument with the five pairs of lamelligerous appendages of *Limulus*.

(The tabular statement is given on the next page.)

<i>Segments.</i>	LIMULUS.		
	<i>Tergites.</i>	<i>Sternites.</i>	<i>Appendages.</i>
1	Cephalothoracic carapace with central and peripheral eyes.	Camerostome (small tubercular sclerite) in front of the mouth.	Small chelæ.
2		The fused pro- and mesothoracic sternites (a narrow elongate sclerite stretching from the mouth to the chilaria).	Chelæ.
3			Chelæ.
4			Chelæ.
5			Chelæ.
6	Narrow emarginate area at the anterior border of the abdominal carapace. No dorsal pits.	The chilaria or paired metastoma, or mesothoracic sternites.	Digging legs.
7		Soft integument and stigmatic pits (muscular), posterior to base of operculum.	Genital operculum.
8		Epistigmatic pair of sclerites and stigmatic pits.	1st gill-book pair projecting.
9	2nd pair of lateral spines. 2nd pair of dorsal pits and entapophyses.	Epistigmatic pair of sclerites and stigmatic pits.	2nd gill-book pair projecting.

Abdominal carapace.

Segments.	SCORPIO.		
	Appendages.	Sternites.	Tergites.
1	Chelicerae.	Camerostome (of Latreille), or upper lip.	Cephalothoracic carapace with central and peripheral eyes.
2	Chelæ.	Obliterated by the mesiad extension of the coxæ of the four walking legs; the two anterior movable, the two posterior fixed. (In Mygale a distinctly marked small prothoracic sternite is followed by a large oval mesothoracic sternite.)	
3	Walking legs.		
4	Walking legs.		
5	Walking legs.		
6	Walking legs.	Pentagonal elongate sclerite or metathoracic sternite.	
7	Genital operculum.	Soft integument.	A separate narrow band-like sclerite.
8	Pectinæ, or pair of comb-like organs; modified gill-book projecting.	Separate small rectangular sclerite.	A separate narrow band-like sclerite.
9	1st gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.

Segments.	LIMULUS.		
	Tergites.	Sternites.	Appendages.
10	3rd pair of lateral spines. 3rd pair of dorsal pits and entapophyses.	Epistigmatic pair of sclerites and stigma- tic pits.	3rd gill-book pair projecting.
11	4th pair of lateral spines. 4th pair of dorsal pits and entapophyses.	Epistigmatic pair of sclerites and stigma- tic pits.	4th gill-book pair projecting.
12	5th pair of lateral spines. 5th pair of dorsal pits and entapophyses.	Epistigmatic pair of sclerites and stigma- tic pits.	5th gill-book pair projecting.
13	6th pair of lateral spines. 6th pair of dorsal pits and entapophyses.	Abdominal carapace. Large and solid sclerite forming the sternum of the "Telson," <i>i.e.</i> of the præ-anal region of potential segmentation, which includes a soft invaginate area on which opens the ANUS.	None.
14	Only in the embryo this segment is separate, and has a 7th pair of lateral spines.		None.
15	Only in the embryo this segment is indicated.		None.
16	These three segments are never expressed and are represented by the præanal region of the telson.		None.
17			None.
18			None.
	Post-anal spine.		

Abdominal carapace.

<i>Segments.</i>	SCORPIO.		
	<i>Appendages.</i>	<i>Sternites.</i>	<i>Tergites.</i>
10	2nd gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.
11	3rd gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.
12	4th gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.
13	None.	A separate broad transverse sclerite devoid of stigmata.	A separate broad band-like sclerite.
14	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
15	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
16	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
17	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
18	None.	Ventral half of a distinct cylindrical sclerite, in which is placed the ANUS.	Dorsal half of a distinct cylindrical sclerite.
			Post-anal spine or sting (a jointed filament in <i>Thelyphonus</i>).

IV. The common characters of the lamelligerous appendages of *Scorpio* and *Limulus*.—When we have once, on the ground of a certain general agreement in structure and of a definite identity in relation to other parts which correspond one to another, started the hypothesis that the lamelligerous appendages of the *Scorpio* agree each to each in their order with the lamelligerous appendages of the *King Crab*, two further proceedings are naturally the consequence. We inquire first of all whether there are any less obvious agreements in the structure of the organs compared which may be brought out and made to give their testimony in favour of our hypothesis, and, secondly, we inquire how can we form a plausible conception of the origin of the two sets of structures from one set of organs present in a common ancestor of *Limulus* and *Scorpio*? this last inquiry having especial value, in that it may lead us to give due value to structures present either in *Scorpio* or *Limulus* which had appeared previously to have no special significance in the matter.

A close comparison¹ of the lamelligerous appendages of *Scorpio* and *Limulus*—including under this head the pectines and the pulmonary books of the former, and the branchial books of the latter—reveals the important fact that they agree closely with one another in the mode in which the lamellæ are set upon the supporting axis.

In all, we find an axis springing from the body wall, transverse to which, on its posterior face, are set a series of lamellæ. In order to compare one of these appendages with another, it is necessary that all should be placed in one and the same position. We must be careful not to compare the anterior aspect of one with the posterior aspect of the other. In the woodcuts, figs. 6 and 7, the posterior face of the appendage as it hangs from its sternal attachment has been represented.

There is no difficulty about determining this face for the pectines of the *Scorpion* or for the branchial appendages of *Limulus*, but the pulmonary books of the *Scorpion* require some consideration. Supposing them to have once been external, we must suppose that, with the gradual invagina-

¹ The account which I give in the text of the lung-books of *Scorpio* differs a good deal from that which is current, due to Joh. Müller as long ago as 1828. I have not had specimens sufficiently well preserved to enable me to determine the relation and possible adhesions of the proper wall of the pulmonary sac (the invaginated sternal surface) to the lamellæ, but have freed the appendage from the investing membrane. I hope to be able by the examination of fresh specimens to give on a future occasion a more thorough account of the pulmonary sacs and lamelligerous appendages of the *Scorpion*.

tion of their surface of attachment, they have become more and more deflected into the cavity of invagination, moving on their fixed base at first backwards, then upwards, and finally forwards. As we now find them (in a spirit specimen!), on viewing the inner surface of the ventral sclerites by removing the terga and viscera, they can be rotated on their hinge line so that they may be made to lie prone forwards, exposing the stigma or opening of the pulmonary recess posteriorly, as in Pl. XXVIII, fig. 1 *a*, or they may be made to lie prone in the reverse direction, hiding from view the stigma, as shown in Pl. XXVIII, fig. 2 *a*, and in the woodcuts, figs. 6 and 7. The position which corresponds with that of the external appendages the pectines and the branchial organs of *Limulus*, when viewed from the posterior face, so as to show (in the case of *Limulus*) the lamellæ, is that in which the lung-book is directed backward so as to hide the stigmatic aperture and is looked at from within the Scorpion's body, that is, by dissecting off the terga, viscera, and muscles.

When the pectines, lung-books, and branchial books are thus placed we find that the lamellæ are not set precisely at right angles upon the axes, but obliquely, so that there is an imbrication of the successive lamellæ. In all three it is the posterior lamella which is uppermost (see Pl. XVIII, fig. 2 and 2 *a* 2 and fig. 10 *l'*). *The imbrication is identical in all.*

As to *number* of lamellæ, we find in the pecten of *Buthus Kochii* eighteen (in other scorpions there are more or less); in the lung-books of some scorpions¹ as many as 130, and in the *Limulus* gill-book as many as 150. These numbers vary slightly, increasing with growth in all probability.

As to *structure* of lamellæ, those of the pecten are more solid and strongly chitinised than those of the other two organs, but are, nevertheless, true lamellæ flattened transversely.

Those of the lung-books are exceedingly delicate plates composed of two closely approximated membranes, between which the blood circulates; they are, in fact, flattened bags. They carry on their free margins a few chitinous spinules (Pl. XXVIII, fig. 8). The lamellæ of the gill-books of *Limulus* are similarly delicate flattened bags with a setose free border. I am not able to institute any comparison of the histological structure of the lamellæ of the Scorpion's lung-book with that of the King Crab's gill-book, for although I have been able to work out that of the latter on

¹ I believe the form in which I counted these to be a species of *Androctonus*.

fresh material, no such opportunity has yet presented itself of investigating the Scorpion.

As to the *shape* of the lamellæ, those of the pecten are narrower and relatively thicker than those of the lung-books or gill-books; the whole eighteen are also more nearly equal to one another in size and shape. In the lung-books the shape differs at the two extremities of the series a little, and in size the proximal laminæ are much larger than the distal. The average shape may be described as that of a broad scythe-blade (Pl. XXVIII, fig. 8) with a narrow base support (*a b*). The lamellæ of the gill-books of *Limulus*, on the other hand, are approximately semicircular in shape, with a wide base of origin (*a b* in fig. 9, Pl. XXVIII). Moreover an important difference, which is explained by the convergence in place of divergence of the axis of the limb relatively to the mid line of the body, is seen when the lamellæ of the gill-book and of the lung-book are compared, in the fact that in the gill-book the proximal laminæ are the smallest (Pl. XXVIII, fig. 10 *l'*), whilst in the lung-book they are the largest.

Further comparison of the grouping and form of the lamellæ is facilitated by the figures on Pl. XXVIII, where fig. 1 and fig. 1 *a*, fig. 2 and figs. 2 *a* and 10, fig. 3 and figs. 3 *a* and 3 *b*, give representations of the three varieties of lamelligerous appendages in a series of identical positions. Fig. 1 should, for comparison with fig. 1 *a*, be looked at by inverting the plate.

The axes which support the lamellæ in the three varieties of lamelligerous limb differ much from one another, but in a manner directly corresponding with obvious functions.

The pecten has a large free axis firmly chitinised, imperfectly divided into two joints. It is flattened by antero-posterior pressure. The function of the pecten is not actually known, but it appears to be tactile. It is not respiratory, and the Scorpion is of terrestrial habit; hence its comparatively solid character and protective development of chitin.

The gill-book of *Limulus* is supported on an axis, which is flattened by dorso-ventral pressure, protection being thus afforded to the otherwise naked and very delicate lamellæ. It is not free except at its extremity, where it exhibits a jointing of separate chitinous plates. Its base is very wide, and is attached, not to a flat sternal surface, but to an out-standing sternal lobe, which extends to the bases of fellow-appendages, and gives rise to a teat-like soft process in the median line (Pl. XXVIII, *m d*, fig. 10). The charac-

ter of this axis is obviously an adaptation to the branchial function of the lamellæ combined with a locomotor function.

The lung-book of *Scorpio* has no locomotor function, and it is protected by the recess of the sternum, in which it lies. It is not tactile, nor is it exposed to desiccation and rough usage, as are the pectines. It is specialised for respiratory purposes. The axis is exceedingly small and simple, for the greater part of its length adherent to the invaginated sternal wall, leaving, however, a small free distal portion (see Pl. XXVIII, fig. 2 *a*). Its walls are quite free from chitinisation, and of great delicacy. It is little else than a horizontal vascular tube supporting the lamelliform bags into which its cavity leads (Pl. XXVIII, 2 *a*, *b*).

Though the axis is here reduced to its simplest expression, it is not possible to overlook in it the representative of the vertically compressed chitinated axis of the pecten, and of the horizontally compressed chitinated axis of the gill-book.

V. Hypothesis as to the mode of origin of the three varieties of lamelligerous appendages in *Scorpio* and *Limulus*.—The view which I have advanced in this memoir as to the practical identity of the gill-books of *Limulus* and the lung-books of *Scorpio* implicitly contains the affirmation that either the structures of *Limulus* have been derived from those of *Scorpio*, or those of *Scorpio* from those of *Limulus*, or that a third (now extinct) form has given rise to both *Limulus* and *Scorpio*. Further, it is to be observed that such extinct form might be more like to *Limulus* than to *Scorpio*, or *vice versa*, in respect of any particular element of structure.

To make a long story as short as possible I may say that, without prejudicing the recognition of the (as I think) well-established morphological identities above pointed out, we may best explain their existence by assuming that an aquatic form breathing the dissolved oxygen of the water inhabited by it, by means of book-like gills, was the common ancestor of *Limulus* and of *Scorpio*. From the book-like gills of this ancestral form the broad series of *Limulus* and the narrower lung-books, *as well as the pectines or combs* of the *Scorpion*, have been derived. The form of the book-like gills of this Arachnid ancestor was probably something intermediate between the three existent modifications of it, and best conceived of, perhaps, by imagining the teeth of the *Scorpion's* "pectinate organs" to become soft and flattened and increased in number (see Pl. XXIX, fig. 1).

To obtain from these the *Limulus* gill we have but to suppose certain definite changes of dimension, the imbrication and character of the lamellæ, and their external position remaining unaltered (Pl. XXIX, figs. 2 *a* and 3 *a*).

To arrive at the book-lungs of the Scorpion, we have to imagine the ventral surface on each side in close proximity to the short appendages carrying the gill-books—to have become deeply cupped or depressed, so that two series of cup-like pits should be formed, a right and a left, a pair being placed in each segment, corresponding to each pair of gill-books. Each cup must have become so large in area and so deep as to embrace within its limits the relatively small adjacent gill-book (XXIX, fig. 2 *b*). Further, when once the gill-book had been involved in this cup-like depression, the walls of the cup must have tended to grow together so as to form a pulmonary chamber with only a narrow slit-like opening to the exterior (Pl. XXIX, fig. 3 *b*), and *pari passu* with this closing in of the cupped area, and the protection of the respiratory lamellæ, the Arachnid must have acquired the power of leaving the water and of breathing the atmospheric oxygen admitted to the damp chamber formed by the cave-like areas of depression.

Whilst framing such a hypothetical account of the way in which the transition from naked "gill-book" to insunken "lung-book" could have taken place, one naturally asks—"Is it not somewhat gratuitous to assume that cupped aræ should form conveniently by the side of the gill-books of the aquatic ancestor, so as to be ready to increase in size, and ultimately draw into themselves, as it were, the gill-books?" "Is there," we are led on further to ask, "any known instance in Arachnida of the formation of cupped aræ on the chitinous surface of the body? If so, can we show in what mechanical relation they are formed? And, lastly, can it be demonstrated that such mechanical relation probably existed in connection with the gill-books of the assumed common ancestor of *Limulus* and *Scorpio*?" If all these questions can be affirmatively answered, then our hypothesis as to the transition of the aquatic Arachnid to the pulmonate condition acquires great plausibility.

The answer to these questions appears to me to have more than ordinary interest, since the formation of cupped aræ on the chitinous surface of the body and the mechanical relations connected with their formation have, as pointed out a few pages back, come to light as demanded by the hypothesis. They exist in *Limulus* itself and in *Thelyphonus*. In *Limulus* there are two great muscles, a right and a left,

inserted into the soft ventral integument near the base of each double gill-plate. These muscles serve (together with others that enter the appendage itself) by their contractions to move the gill-plates in the water and so aid in aquatic respiration. The position of the insertion of each muscular mass is marked by a deep funnel-like depression of the integument. From the external surface this depression appears as a "stigma," which we have already described as the parabranchial stigma. The funnel-like depression has a narrow mouth which is often as much as half an inch in length. Internally the invaginated cuticle stands up as a flexible tendon clothed with fibrous tissue and giving attachment to the muscle already mentioned.

In *Limulus* we find a pair of these "muscle-stigmata," right and left behind the genital operculum, and a pair (right and left) behind each of the lamelliform fused appendages which carry the gill-books.

We have only to suppose the appendages carrying the gill-books *not* to have fused as yet in the middle line, and the muscular stigmata to have become greatly developed (perhaps by increased development of the muscle aiding in aquatic respiration when the appendage itself grew small and therefore less efficient) and we have at once the gill-book sinking within the area of the stigmatic pit, Pl. XXIX, fig. 2*b*.

A very important feature in the supposed further development is the correspondence of the atrophy of the muscle (which atrophy is required to fit in with our hypothesis, and to convert the muscle-pit into a pulmonary sac) with the changes in the structures which would necessarily result were the physiological conditions gradually to become such as to favour aërial in place of aquatic respiration. The violent agitation of the gills by the muscle attached to the stigmatic pit would become useless, supposing an exposure of the gill-lamellæ to the atmosphere became by degrees habitual with the ancestral Arachnid. In proportion as these hypothetical creatures acquired the habit of aërial respiration—the deepening and arching in of the stigmatic pit would be favoured, and the atrophy and final disappearance of the muscle which was attached to its inner surface, and mechanically brought it into existence, would also be directly promoted.

A further confirmation of the view now advanced is found in the remarkable East Indian Arachnid *Thelyphonus*. This Arachnid has not four pairs of lung-sacs like *Scorpio*, but only two pairs, corresponding to the two foremost lungs of

Scorpio, and to the second and third gill-book-pairs of *Limulus* (woodcut, figs. 12, 13, 14). Nevertheless, as we have seen in a previous section of this Essay, the *four* segments of the abdomen posterior to these are *each marked by a pair of shallow stigmata placed in line with the orifices of the pulmonarg sacs of the two anterior segments, msg.* When the internal structure corresponding to these parts is examined, it is found that a large muscle (similar to the similarly placed muscle of *Limulus*) is inserted into each of the four right and four left stigmata in the segments posterior to the pulmonary sacs (woodcut fig. 14, *m.*) The two segments into which the two pairs of pulmonary sacs are sunk, have *no such muscles*. The pulmonary sacs are, therefore, to all appearance, enlarged muscular stigmata, from which their former muscles have disappeared by disuse and atrophy.

VI. The Entosternite.—Leaving now the comparison of segments and appendages, which is undoubtedly the most important element in determining our judgment as to the affinity of *Limulus* with *Scorpio*, we come to the consideration of a number of other structures, which we shall find some more and some less favorable to the hypothesis of a close relationship between the two animals.

Connected with the exoskeleton and locomotor system is that remarkable development of an endoskeleton in the Arachnida, which Straus Durkheim put forward in the passage cited at the commencement of this article, as one of the leading characteristics of the class and one of the obvious features in which *Limulus* shows itself to be a true Arachnid.

As already remarked, in speaking of the entapophyses and parabranchial stigmata, *Limulus* shows a marked tendency to the development of cartilage and fibro-cartilage by the modification of its connective substance at certain points and in certain areas.

The most striking result of this tendency, is the formation of a large fibro-cartilaginous plate which lies in the cephalothoracic region between the alimentary canal above and the nerve collar below, and unconnected by hard parts with any portion of the exoskeleton. It is represented of the natural size as seen from the ventral (sternal) aspect in fig. 7, Pl. XXVIII. It has been previously figured by Van der Hoeven (12), whose figure is not very accurate, and is copied by Owen (7).

This body is the base of origin of a large number of muscles, and may be regarded as an enlargement and

interlacing of their respective tendons. In the figure, nothing but the skeletal structure, cleaned of its muscles, is represented.

In Scorpio, a similarly shaped loose skeletal piece is found, which gives attachment to muscles in the same way and has a similar relation to the ventral nerve-mass and artery, by which in Scorpio it is perforated (Pl. XXVIII, figs. 6 and 6 *a*). The corresponding body in Mygale is (Pl. XXVIII, figs. 5, 5 *a*) more closely similar in form to that of Limulus than is that of Scorpio.

In order to make a close comparison of these Entosternites, it will be necessary to determine exactly the insertions of the muscles to which they give origin; and further, to ascertain how far the histological structure of those of Scorpio and Mygale agrees with that of Limulus. The results of this investigation I hope to make the subject of a future publication. In the meantime the close correspondence in general character of the three Entosternites figured on Pl. XXVIII cannot escape notice, and fully justifies the importance which Straus Durkheim attached to them. The two pairs of tendinous outgrowths right and left of the central plate in Limulus correspond with the three pairs seen in Mygale, whilst the deep anterior notch in the latter corresponds with the shallower excavation in Limulus, in which the number 7 is placed in the drawing, and in which in the animal itself the bend of the alimentary canal is placed, the mouth being actually below the central region of the plate, so that the alimentary canal passes first forwards beneath the plate and is then reflected so as to pass backwards whilst resting on the upper surface of the plate.

Whilst of this as of so many other structures of the Arachnida (such as the lung-books, &c.) which have been compared in the present memoir with structures in Limulus, a renewed and critical examination is absolutely needed, yet we have sufficient ground, even in our present incomplete knowledge, for concluding that the agreement as to them presented by the two animals is a very close one.

In no Crustacean is a free entosternite at all similar to the organ under discussion known. The apodemes of the sternal surface of Decapodous Crustacea do not resemble it in form though of a similar function. The nearest approach to it is seen in the rod-like skeletal organ found in the abdomen of Lepidoptera, and described by Leydig ('Bau des Thierischen Körpers,' Atlas, pl. vi, fig. 1). Its shape and position are very different, however, from the

entosternites of *Limulus* and other Arachnida. It agrees with these only so far as that it is a free internal skeletal piece.

In the abdominal region of *Limulus* small loose fibro-cartilages, similar in nature to the Entosternite, are found, connected with the tendons of muscles. I have isolated four such pieces. They are mentioned by Straus Durkheim.

(To be continued.)



E. Roy Lankester del. M. P. Parker lith. A. Stone del. ad nat.

LIMULUS & SCORPIO.

West Newman & Co. imp.

JOURNAL OF MICROSCOPICAL SCIENCE.

EXPLANATION OF PLATES XXVIII AND XXIX, Illustrating Professor Lankester's Memoir on "*Limulus* an Arachnid."

PLATE XXVIII.

FIG. 1.—Right pectinate appendage (eighth segment) of *Buthus Kochii*, anterior face. This figure should be turned so that the pectinate border is uppermost, in order to compare with Fig. 1 *a l'*, proximal lamella; *lx.*, distal lamella (eighteenth).

FIG. 1 *a*.—Similar view of the right lamelligerous appendage of the eleventh segment of the same animal for comparison with Fig. 1. *l'*, proximal lamella; *lx.*, distal lamella (one hundred and thirtieth; the full number of lamellæ are not indicated by the lines in the drawing); *m.*, membrane attaching the axis of the appendage to the superior margin of *st.*, the stigmatic aperture. The appendage is represented as seen when all other structures are removed from the interior of the Scorpion's body, it is reflected forwards so as to rest with its proper posterior face downwards on the inner surface of the sternite in front of the stigma. The delicate membrane which bounds the pulmonary sac and represents the invaginated integument is removed.

FIG. 2.—Right pectinate appendage of *Buthus Kochii*, posterior face; letters as in Fig. 1.

FIG. 2 *a*.—Similar view of the right lamelligerous appendage of the eleventh segment of *Buthus Kochii*, for comparison with Fig. 2; letters as in Fig. 1 *a*, except *b*, the canal-like axis which supports the lamellæ.

FIG. 3.—View of the inferior margin of the right pectinate appendage of *Buthus Kochii*, so placed as to show the imbrication of the lamellæ; letters as in Fig. 1.

FIG. 3 *a*.—Similar view of the right lamelligerous appendage of the eleventh segment of *Buthus Kochii*, for comparison with Fig. 3; letters as in Fig. 1 *a*.

FIG. 3 *b*.—Similar view of the right lamelligerous appendage of the eleventh segment of *Limulus polyphemus* for comparison with Fig. 3 and 3 *a*: *l'*, proximal lamella; *lx.*, one hundred and fiftieth lamella; *ex.*, external lappet (exite) of the bifid distal prolongation of the appendage.

FIG. 4.—View of the sternal surface of the cephalothorax of *Limulus polyphemus*, from which the five hinder pairs of appendages have been detached. *sf.*, subfrontal sclerite; *Ch.*, the first pair of appendages or chelicerae; *cam.*, the upper lip or camerostome; *M.*, the mouth; *pmst.*, the thoracic promesosternite (representative of pro- and mesosternite as separately developed in the spiders, see woodcut, fig. 9); *metst.*, thoracic metasternite or chilaria, homologous with the pentagonal metasternite of Scorpion, see woodcut, fig. 8, *met*.

EXPLANATION OF PLATES XXVIII AND XXIX—*continued*.

FIG. 5.—Entosternite of bird's-nest spider (*Mygale*, sp.), dorsal face.

FIG. 5 *a*.—The same, neural face.

FIG. 6.—Entosternite of a Scorpion (*Buthus*, sp.), posterior face.

FIG. 6 *a*.—The same, neural face.

FIG. 7.—Entosternite of *Limulus polyphemus*, neural face. Compare with Fig. 5 *a* and Fig. 6 *a*.

FIG. 8.—A single lamella of the right lamelligerous appendage of the eleventh segment of *Buthus Kochii*, formed by two closely adherent plates: *a. b.*, the base or line of attachment. Note the marginal setæ.

FIG. 9.—A single lamella of the right lamelligerous appendage of the eleventh segment of *Limulus polyphemus*, for comparison with Fig. 8: *a. b.*, the base or line of attachment. Marginal setæ are present, but more numerous than in Fig. 8.

FIG. 10.—View of the posterior face of the conjoined pair of lamelligerous appendages of the eleventh segment of *Limulus polyphemus*: *st.*, soft sternal lobe or plate which unites the two appendages; *md.*, median process or soft papilla of the sternal plate; *epst.*, epistigmatic sclerite; *stg.*, para-bran- chial stigma (invagination to give attachment to the thoraco-bran- chial muscle); *app. m.*, protractor muscle of the appendage, seen through the soft integument; *l.*, branchial lamellæ; *l'*, the proximal lamella; *app.*¹, the proximal division of the appendage carrying the lamellæ and extending beyond them; *app.*², *app.*³, *app.*⁴, second, third, and fourth sclerites, forming the jointed axis of the distal prolongation of the appendage; *ex.*, exite or outer ramus of the appendage.

FIG. 11.—View of the pair of lamelligerous appendages of the ninth segment of *Limulus polyphemus*, seen from in front. The chitinised integument has been removed from the surface of the proximal portion of the appendages, so as to expose the bases of the hollow lamellæ, and the soft integument of the median sternal area; and the retractor muscles have also been removed so as to expose the inner face of the corresponding integument of the posterior face, and the insertions of the thoraco-bran- chial muscles: *st.*, sternal lobe; *stm.*, thoraco-bran- chial muscle of the left side; *Bl.*, bases of the laminæ, open to the branchial blood-vessels.

FIG. 12.—A semi-diagrammatic view of one of the respiratory appendages of a Scorpion, to show *Bl.*, the bases of the lamellæ exposed, as in *Bl.*, fig. 11, by the removal of the integument of the axis, the remnants of which are seen at *m*. The drawing further shows the gradual narrowing of the bases of the laminæ in the series as the distal region is approached until the free projecting portion of the axis (*x*) is reached; *l.*, proximal lamella.

FIG. 13.—A tendon-sac of *Limulus polyphemus* detached from the para-bran- chial stigma, the homologue of the pulmonary sac of Scorio.

PLATE XXIX.

The drawings on this plate are diagrammatic, and illustrate the hypothesis as to the derivation of the lamelligerous appendages of *Limulus* and Scorio from a common ancestral form. All the figures, except 4, 5, 6, present the appendages as seen when the ventral surface of the animal is facing the observer.

FIG. 1.—Hypothetical intermediate form. *R.* axis of appendage; *l.*

